Megalobrachium poeyi (Crustacea, Decapoda, Porcellanidae): Comparison between Larval Development in Atlantic and Pacific Specimens Reared in the Laboratory[1]

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THE PORCELLANID CRAB GENUS *Megalobrachium,* which contains 11 known species, is confined to the new world. *Megalobrachium poeyi* (Guérin-Méneville, 1855) is, at present, the only member of this mainly tropical, intertidal genus with forms on both sides of the Panamanian isthmus. Originally considered an Atlantic species, it was apparently not collected on the Pacific coast until 1926 (see Boone, 1931, p. 150; Haig, 1960, p. 339) and is still considered uncommon on that side of the continent (Haig, 1960, p. 215) with a range restricted to Panama and Costa Rica (Haig, 1968, p. 72). The male and female crabs collected on the Pacific coast and reported herein bring the known total of Pacific specimens to 15.

Megalobrachium poeyi has no known analogous or geminate species, although several other species have closely related forms on each side of Panama (e.g., *M. erosum* and *M. mortenseni,* see Haig, 1962, p. 191).

Because fossils are lacking, it is not known from which side of the continent *M. poeyi* originally came, and whether the species was an early or recent migrant. It is widely distributed throughout the Caribbean Sea. Its apparent rarity and restricted range on the Pacific coast suggests that the species originated in the Atlantic area. On the other hand, immigration from the Pacific and subsequent radiation throughout the Caribbean cannot be discounted. The scarcity of Pacific specimens might be due to insufficient collecting.

No larvae have been described for any species of *Megalobrachium.* A comparison of the larvae from the Atlantic and Pacific specimens of *M. poeyi* is, therefore, desirable for identification, as well as for determination of whether variation exists in the two populations now geographically separated but presently considered conspecific. Accordingly, the complete development in laboratory culture of larvae of both an Atlantic and a Pacific specimen of *M. poeyi* is described and illustrated in this paper. The larvae of the two specimens are compared with each other and discussed in reference to Lebour's (1943) identification scheme based on telson features in porcellanid larvae. The taxonomic position of the adults is considered, based on the results obtained by rearing the larvae.

MATERIALS AND METHODS

An ovigerous female crab collected from the Pacific side of Panama at Punta Paitilla, December 31, 1968, was shipped by air to the Rosenstiel School of Marine and Atmospheric Science in Miami, Florida. The crab was isolated in nonflowing seawater in a 19-cm-diameter glass bowl until hatching occurred on January 26, 1969.

The Atlantic larvae were produced by an ovigerous female collected from a cluster of phragmatopomid worms at Northwest Point, Key Biscayne, Florida, May 21, 1969. This crab was isolated as above and hatching occurred on May 27, 1969.

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A numbered series of 120 larvae from each female was reared. The remaining larvae, about 100 from each female, were preserved in 70 percent ethanol.

In both numbered rearings a single zoea was placed in each compartment of 24-compartmented plastic trays. Each compartment was filled with about 80 cc of Biscayne Bay seawater which was filtered through Pyrex glass wool. Larvae were fed *Artemia salina* nauplii in amounts sufficient to ensure that nauplii always remained in the compartments; the presence of nauplii was checked before the water was changed. I originally planned to rear both numbered series of larvae at 10°, 15°, 20°, 25°, and 30° C, but three of the controlled temperature units (CTU) varied from the preset temperatures (see "Variations in Temperature and Salinity"). Water was changed every second day at 10° and 15° C, and every day at higher temperatures. Larvae were maintained in the dark, but were subjected to ambient illumination whenever they were removed from the temperature units.

Descriptions of larvae were based on material examined from all temperatures. Dead larvae and exuviae were preserved in 70-percent ethanol. Individual slides of whole larvae, or appendages dissected in 40-percent lactic acid from larvae or exuviae, were mounted in Turtox CMC-S, a staining, water-miscible, mounting medium. Drawings were then made with a Wild M-20 binocular compound microscope with drawing tube attachment. All measurements were made with a Lafayette slide micrometer. In the zoeae, carapace lengths were measured from the anterior margin of the eyes, to the points of insertion of the posterior carapace spines. In the megalopae, carapace lengths were measured from the frontal regions to the posterior edges of the carapaces; carapace widths were measured across the widest part of the carapaces. The sizes given are the arithmetic average for the number of specimens examined.

VARIATIONS IN TEMPERATURE AND SALINITY

While the Pacific series was being reared, the 25° C CTU varied irregularly from 24°–26.5° C; the 30° C unit failed completely on the 11th day of the program, dropping from 30° C to 24.5° C over a 48-hour period, before rising again to a steady 28° C which temperature was then maintained until the end of the Pacific series experiment. This unit failure is noted in Figure 1 on the 30° C graph for Pacific larvae. Salinity for the entire series varied from 32.0–34.7 ‰ during the experiment.

In the Atlantic series, four of the five CTU functioned correctly (± 0.5° C of desired temperature), but the 10° C unit fluctuated between 5° and 8° C. Salinity varied between 31–32.5 ‰ for the first 20 days of the program, then dropped to 26.6 ‰ for 2 days after a period of heavy rains in the bay, before rising again to 28 ‰ and then to 31 ‰ in 2 days. The program of water changes exposed only the larvae at 20° C to the 26 ‰ salinity; the rest of the series never dropped below 28 ‰ salinity (see Fig. 2).

The spent females, the males collected with them, plus a complete larval series from each female were deposited in the museum of the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami (UMML 32:4183, 32:4184, 32:4185, 32:4186).

REARING EXPERIMENT

Megalobrachium poeyi hatches as a prezoea in both its Atlantic and Pacific forms, this stage lasting about 1 hour; this form is not described here. There are two zoeal stages and a megalopal stage. The rearing results for both series at each temperature are given in Figures 1 and 2 and Table 1. The failure of the CTU to maintain 30° C began just as the second stage zoeae in the Pacific series were molting to megalopae. The salinity drop on the Atlantic series occurred 9 days after the zoeae being maintained at 20° C had molted to stage II. The effect these variations had on subsequent stages cannot be determined since the Atlantic series was originally being reared in water of lower salinity than the Pacific series and, in the end, had a longer developmental period than the latter. This longer period, in itself, might be due to the lowered salinity or merely to variation in the duration in the amphi-Panamanian forms. The temperature failure at 30° C might have

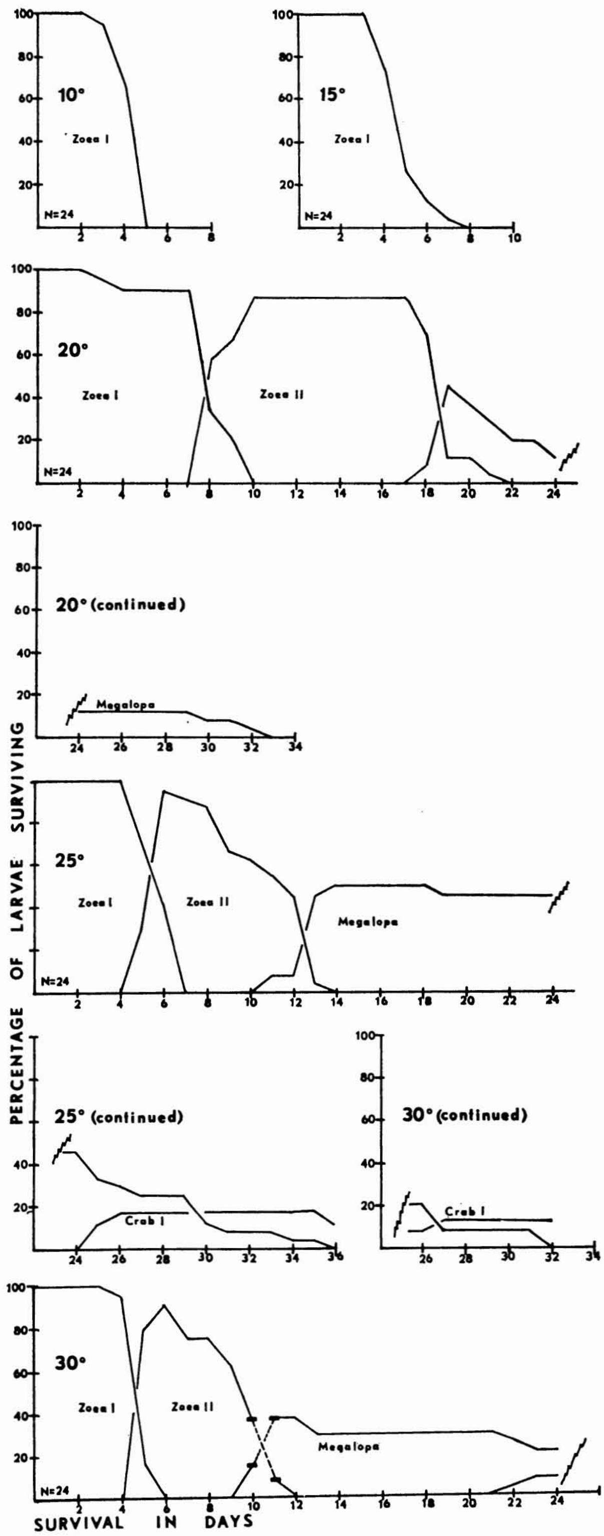

FIG. 1. Percentage and duration of survival of larvae of Pacific specimens of *Megalobrachium poeyi*, reared under laboratory conditions. Hatched line at 30° C denotes period of temperature fluctuation (see text). N is number of larvae reared at each temperature (C°) in the series.

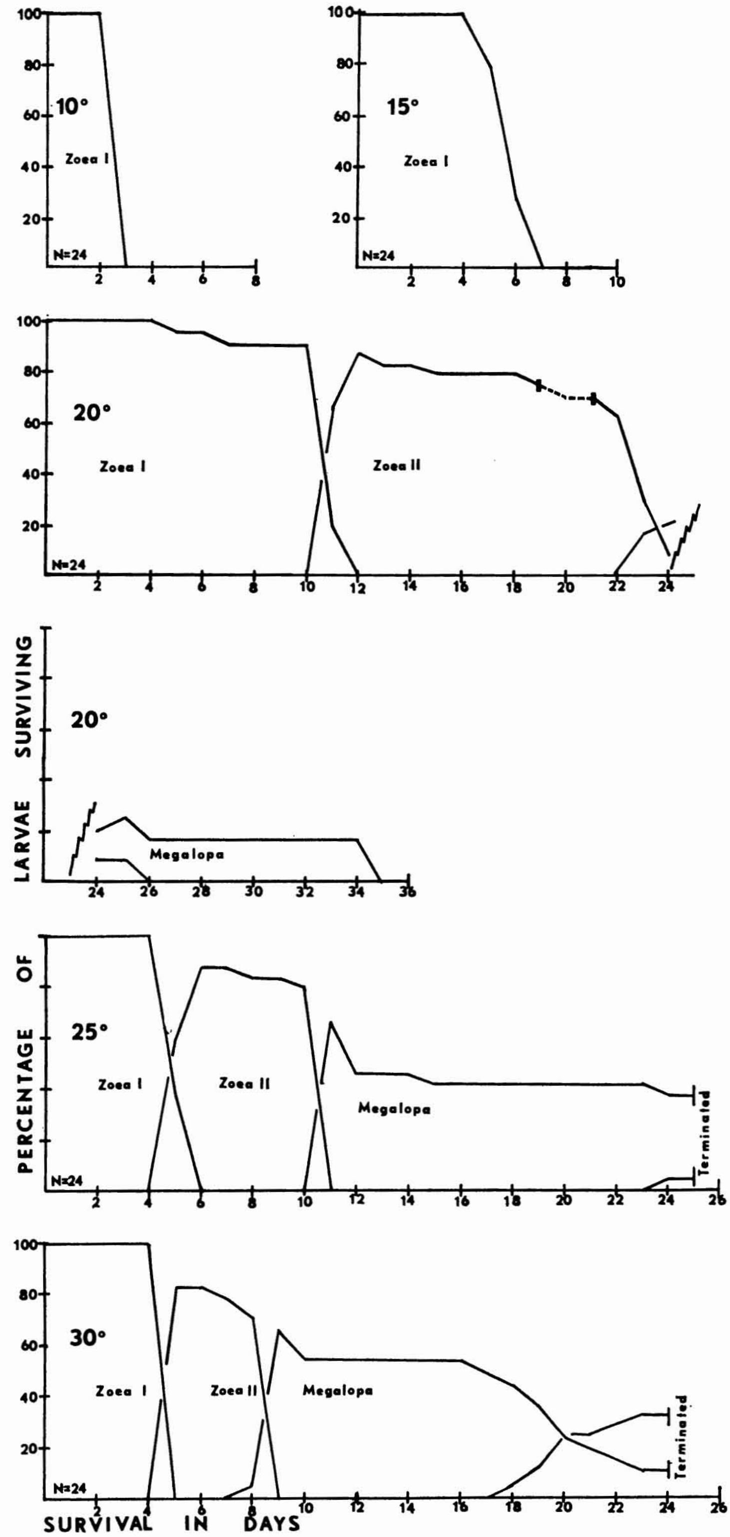

FIG. 2. Percentage and duration of survival of larvae of Atlantic specimens of *Megalobrachium poeyi,* reared under laboratory conditions. Hatched line at 20° C denotes period of salinity fluctuation (see text). N is number of larvae reared at each temperature (C°) in the series.

TABLE 1

DURATION OF LARVAL STAGES FOR *Megalobrachium poeyi*

TEMPERATURE	MINIMUM NO. OF DAYS FROM HATCHING TO SUCCEEDING STAGE			MINIMUM DURATION (in days) IN EACH STAGE			MAXIMUM DURATION (in days) IN EACH STAGE		
	MOLTED TO Z-II	MOLTED TO MEG.	MOLTED TO C-1	ZOEA I	ZOEA II	MEGALOPA	ZOEA I	ZOEA II	MEGALOPA
Atlantic Form									
20°	11	23	N/A	10	12	(12)	11	13	(?)
25°	5	11	24	4	5	13	5	7	(?)
30°	5	8	18	4	3	9	4	5	15
Pacific Form									
20°	8	18	N/A	7	9	(14)	9	12	(?)
25°	5	11	25	4	5	12	5	8	14
30°	5	10	22	4	5	11	5	6	14

NOTE: Series at 10° and 15°C remained as Zoea I until death. Minimum and maximum duration refers only to larvae attaining subsequent stage. N/A, not attained; ( ), terminated in stage without further molt.

affected survival or molting ability of Pacific megalopae because only three of 12 attained first crab stage, whereas, in the Atlantic series, 10 megalopae of 18 reared at this temperature attained first crab stage. Though larvae in both series survived well at temperatures of 20° C and higher, they encountered greatest mortality in the molt to megalopa. As shown in Figures 1 and 2, the period immediately before and after this molt appears critical and 50-percent mortality occurred in both series during this time. It is also evident from Table 1 that 25° C proved to be the most favorable temperature in the series at which to rear both forms, because the duration in each stage, as well as minimum length of time required to attain each stage, was almost exactly the same in the Pacific and Atlantic forms. Larvae reared at 15° C and below, as in most other laboratory-reared tropical porcellanid zoeae, did not progress beyond the stage I zoeae (see Gore, 1968, 1970).

DESCRIPTION OF THE LARVAE

The following description is based on larvae obtained from the Pacific adult. The larvae from the Atlantic, for the most part, are identical to those from the Pacific. However, notable variations in the Atlantic larvae are indicated in the descriptions as [A:] followed by the noted discrepancy (e.g., [A: 6–21]). These variations and their implications will be discussed at length below.

FIRST ZOEA

Carapace Length

Carapace length is 1.01 mm [A: 1.41 mm].

Number of Specimens Examined

Fifteen [A: 10] specimens were examined.

CARAPACE (Figs. 3 and 4, *A*): Typically porcellanid. Long rostral spine about 2.5× [A: 2.9×] carapace length, curved as illustrated, armed with five to seven [A: 12–14] spinules ventrally. Posterior carapace spines about 1.5× carapace length [A: 2.0×], armed with five (range 4–6) [A: 9–11] tiny spinules ventrally and medially. A pair of fine setae over

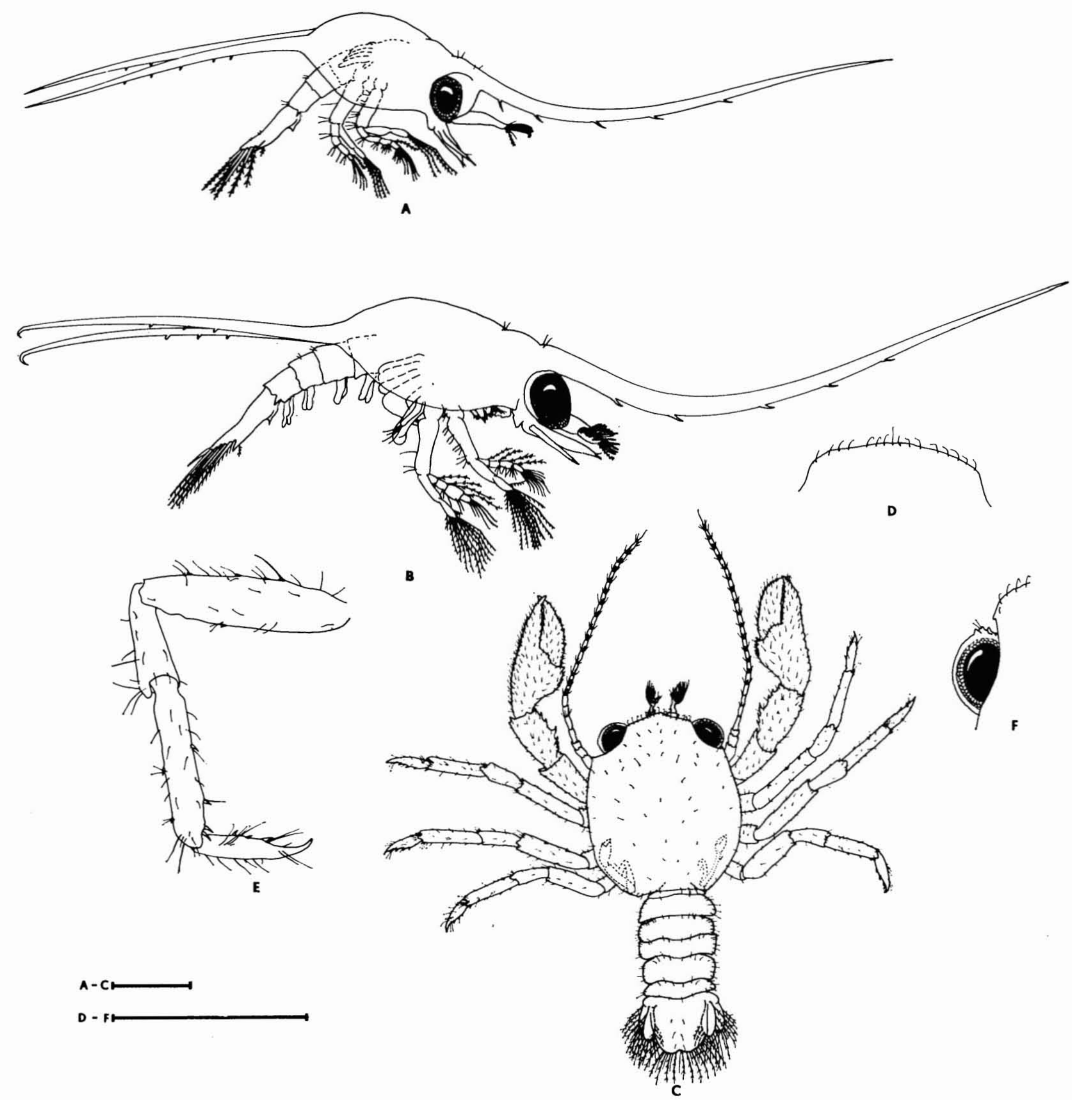

FIG. 3. The zoeal and megalopal stages of *Megalobrachium poeyi* (Guerin), Pacific specimens. *A,* first zoea; *B,* second zoea; *C,* megalopa; *D,* frontal region, megalopa; *E,* first walking leg; *F,* eye detail. Scale lines equal 0.5 mm.

eyes, another pair on notch formed at insertion of rostral spine. Eyes sessile.

ANTENNULE (Figs. 5 and 6, *A*): Simple flabellate rod; three aesthetascs, one large, two smaller setae.

ANNTENNA (Figs. 5 and 6, *B*): Exopodite a slender rod slightly longer [A: ca. 1/4×] than endopodite; a single seta 1/4 way from tip. Endopodite thicker than exopodite, one subterminal seta.

MANDIBLES (Figs. 5 and 6, *C*): Asymmetrical dentate processes; right with large tooth as shown, left with extended molar process. No palp.

MAXILLULE (Figs. 5 and 6, *D*): Endopodite a single segment attached to endite; four ter-

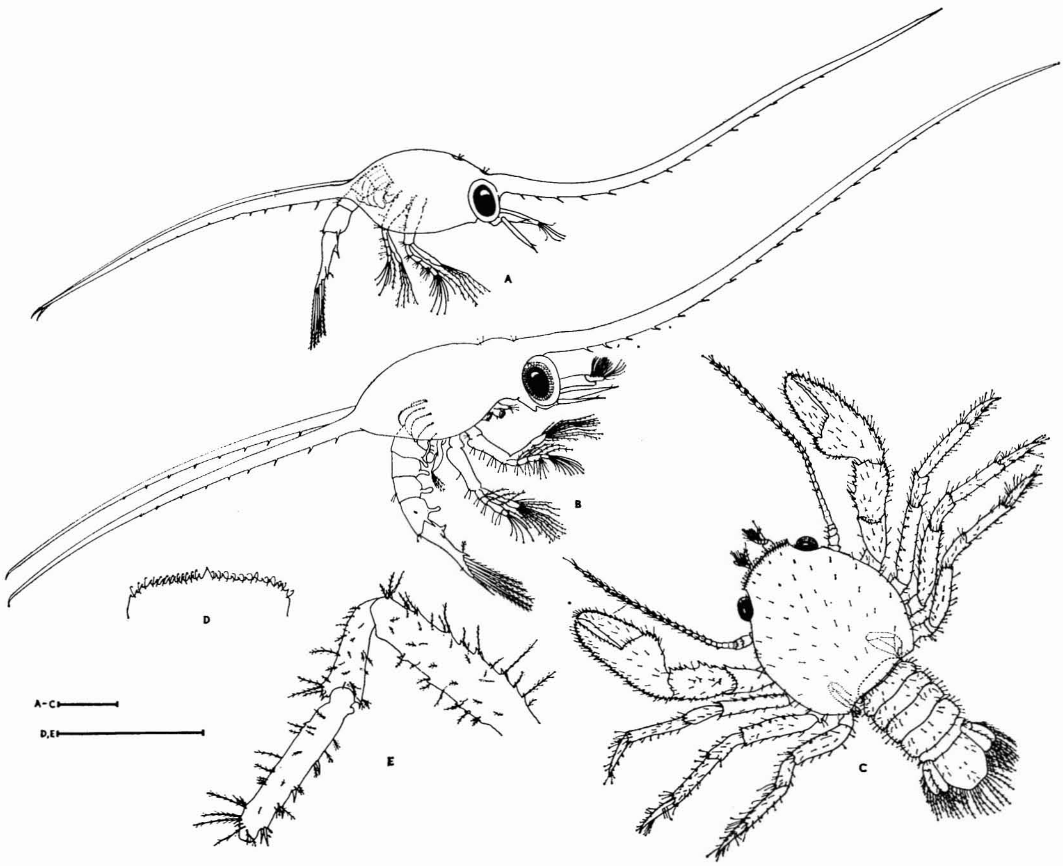

FIG. 4. The zoeal and megalopal stages of *Megalobrachium poeyi* (Guerin), Atlantic specimens. *A*, first zoea; *B*, second zoea; *C*, megalopa; *D*, frontal region, megalopa; *E*, first walking leg (dactyl omitted). Scale lines equal 0.5 mm.

minal, one fine subterminal setae. Basal and coxal endites with six, three, and six, two spines and setae, respectively.

MAXILLA (Figs. 5 and 6, *E*): Endopodite unsegmented; five terminal, three subterminal setae. Basal endite with seven (occasionally eight), seven [A: 7–8, 8–7], coxal endite with seven, four, or five [A: 7–8, 4–5] processes on proximal and distal lobes, respectively. Scaphognathite with two terminal, four lateral [A: 4–5] setae, plus one long plumose apical seta. All processes placed as illustrated.

MAXILLIPED 1 (Figs. 5 and 6, *F*): Coxopodite with two setae (rarely one). Basipodal ventral setae progressing distally 2, 2, 3, 3. Endopodite four-segmented; setae ventrally, 3, 3, 2 + 5 (rarely 6), 9, plus one long plumose seta dorsally on last segment. Small hairs dorsally on segments two, three. Exopodite two-segmented; four natatory setae.

MAXILLIPED 2 (Figs. 5 and 6, *G*): Coxopodite naked. Basipodite ventral setae progressing distally 1, 2. Endopodite four-segmented; ventral setae progressing distally 2, 2, 1 + 2, 5, plus one long plumose seta dorsally on last segment. Fine hairs dorsally on segments two, three. Exopodite two-segmented; four natatory setae.

MAXILLIPED 3 (Figs. 5 and 6, *H*): A small naked double bud in early stages. Future exopodite larger than endopodite. Appendage enlarges as zoea progresses toward second stage.

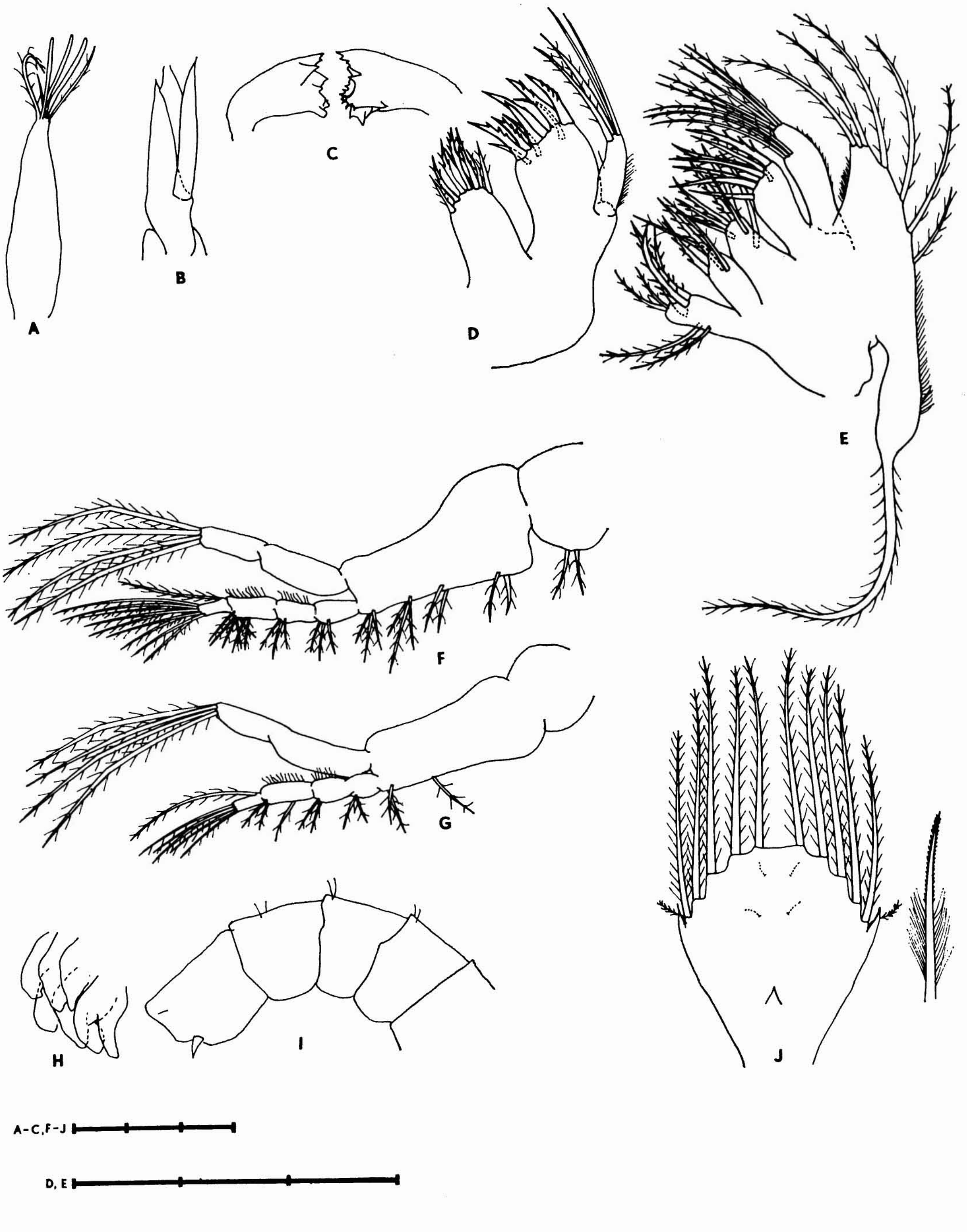

FIG. 5. *Megalobrachium poeyi* (Guerin), Pacific specimen. First zoeal appendages. *A,* antennule; *B,* antenna; *C,* mandibles; *D,* maxillule; *E,* maxilla; *F,* maxilliped 1; *G,* maxilliped 2; *H,* maxilliped 3 and pereiopods, early stage; *I,* abdomen; *J,* telson and setal detail. Scale lines equal 0.3 mm.

PEREIOPODS (Figs. 5 and 6, *H*): Simple buds; enlarge as stage progresses toward second zoea.

ABDOMEN (Fig. 5, *I*): Five somites; paired dorsal setae as shown. Last somite with distinct lateral spine.

PLEOPODS: Absent throughout stage though primordia seen in late stage I.

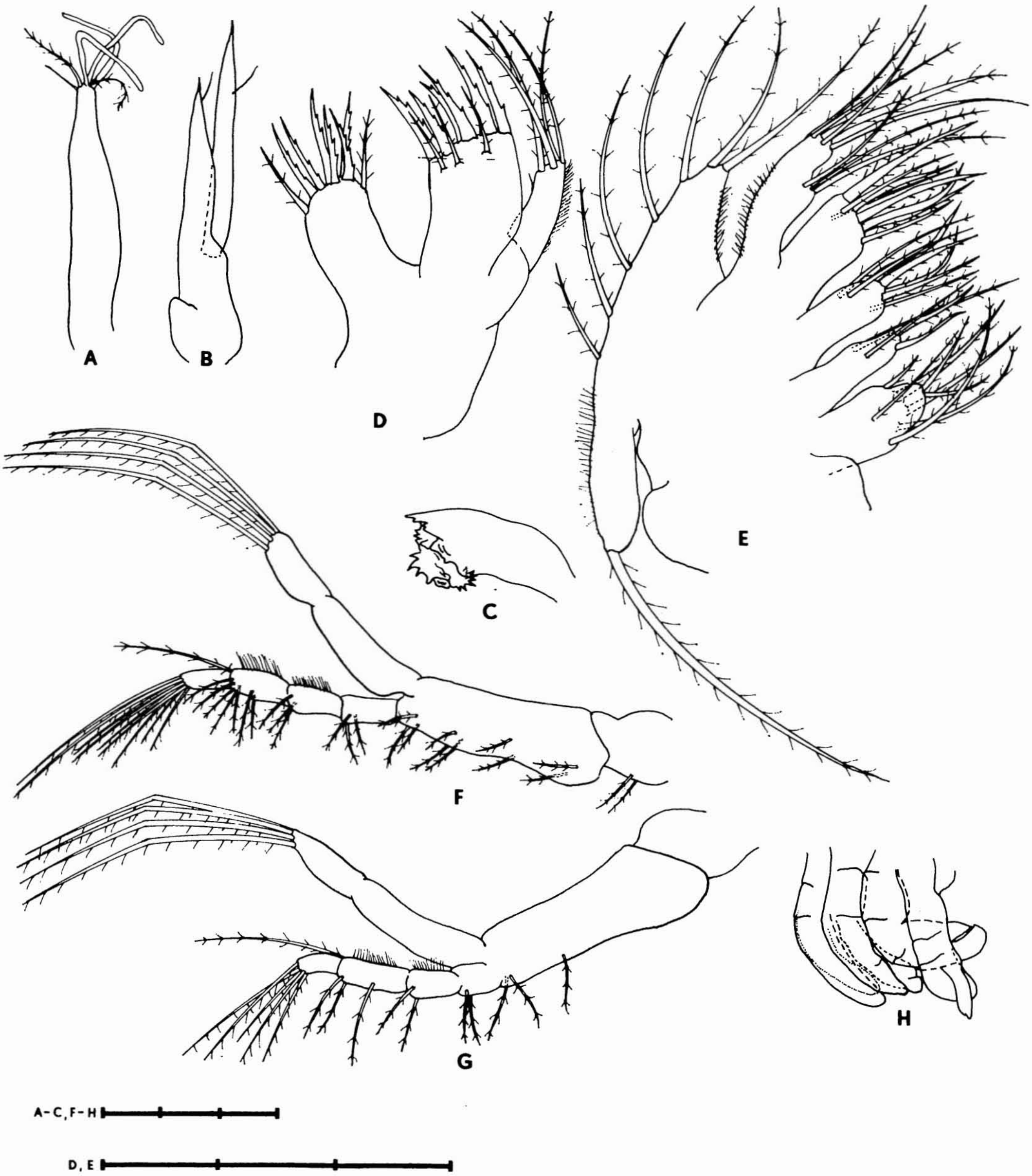

FIG. 6. *Megalobrachium poeyi* (Guerin), Atlantic specimen. First zoeal appendanges. *A,* antennule; *B,* antenna; *C,* mandible; *D,* maxillule; *E,* maxilla; *F,* maxilliped 1; *G,* maxilliped 2; *H,* maxilliped 3 and pereiopods, early stage. Scale lines equal 0.3 mm.

TELSON (Fig. 5, *J*): Seventh pair of processes (fifth pair plumose setae) located on central prominence. Prominence appearing naked but under high magnification several minute hairs visible. Two pair fine hairs dorsally on middle of telson proper. One small seta located next to each large lateral spine. Plumose setae (processes 3–7) appear serrate at tip, but without distinct spinules (see Fig. 5, *J* detail). Anal spine present. [A: similar in all respects, but larger.]

COLOR: Zoea transparent. Distal tip of rostral spine orange; rostral spinules red in reflected light. Eyes iridescent pale blue-green. Red chromatophore on mandibular and maxillary area. One large orange chromatophore on basipodite of each maxilliped. Diffuse orange coloring on pereiopod buds and maxilliped 3. Posterior carapace spines transparent.

SECOND ZOEA

Carapace Length

Carapace length is 1.2 mm [A: 1.6 mm].

Number of Specimens Examined

Ten [A: 8] specimens were examined.

CARAPACE (Figs. 3 and 4, *B*): Now larger, more inflated than previous stage. Rostral spine up to 1.7× [A: 3.5×] carapace length, armed ventrally with four to seven [A: ca. 18 decreasing in size distally] spinules. Posterior carapace spines about 1.6× [A: 2.0] carapace length; three to four [A: 8–10] spinules ventrally and medially. Dorsal setae on carapace unchanged. Eyes mobile.

ANTENNULE (Figs. 7 and 8, *A*): Biramous; endopodite with aesthetascs progressing distally 3, 3, 3, 3, 2, plus four terminally and a plumose seta. Exopodite rounded, naked. Setae at junction of endopodite and exopodite, and on basal medial projection of protopodite as illustrated.

ANTENNA (Figs. 7 and 8, *B*): General form similar to stage I. Exopodite now ½ [A: little longer than ½] length of endopodite; one subterminal seta persists.

MANDIBLES (Figs. 7 and 8, *C*): Larger; now distinctly dentate plus molar processes as shown. Both with unsegmented palp.

MAXILLULE (Figs. 7 and 8, *D*): Endopodite setae as in stage I; may have small subterminal seta as shown [A: seta present]. Coxal and basal endites each with 10 processes as shown.

MAXILLA (Figs. 7 and 8, *E*): Endopodite indistinctly segmented [A: appears segmented]; setae as in stage I. Coxal endite as illustrated; proximal lobe 10 [A: 10–11], distal lobe 6 [A: as shown] processes. Basal endite, proximal lobe 8 [A: 10], distal lobe 10 processes. Scaphognathite with 19 [A: 20] setae around edge plus apical seta.

MAXILLIPED 1 (Figs. 7 and 8, *F*): Endopodite as shown, setae as in stage I. Fine hairs dorsally on each segment now replaced by single plumose seta. Exopodite with 12 natatory setae.

MAXILLIPED 2 (Figs. 7 and 8, *G*): Endopodite setae as in stage I, with additional dorsal seta on each segment as shown; third segment much enlarged. Exopodite with 12 natatory setae.

MAXILLIPED 3 (Figs. 7 and 8, *H*; 7, *J*): Exopodite indistinctly segmented [A: appears obscurely two-segmented under high magnification]; four terminal setae. Endopodite longer, larger, increasing to twice exopodite size by end of stage II; naked. One Pacific specimen had two strong setae as shown.

PEREIOPODS (Fig. 7, *I*, *J*; 8, *H*): Small, indistinctly segmented at beginning of stage; legs 1, 5 incompletely chelate. Gill buds present. Pereiopods and gills continue development throughout stage, former assuming segmentation, latter enlarging noticeably. Entire mass protrudes from under carapace just before molt to megalopa.

PLEOPODS (Figs. 3 and 4, *B*): Buds present; their length decreasing distally on abdominal segments two through five. Buds elongate, becoming indistinctly segmented as stage progresses toward megalopa.

TELSON (Fig. 7, *K*): Seventh process (fifth plumose seta) on central prominence; median spine now present here. Other setae dorsally,

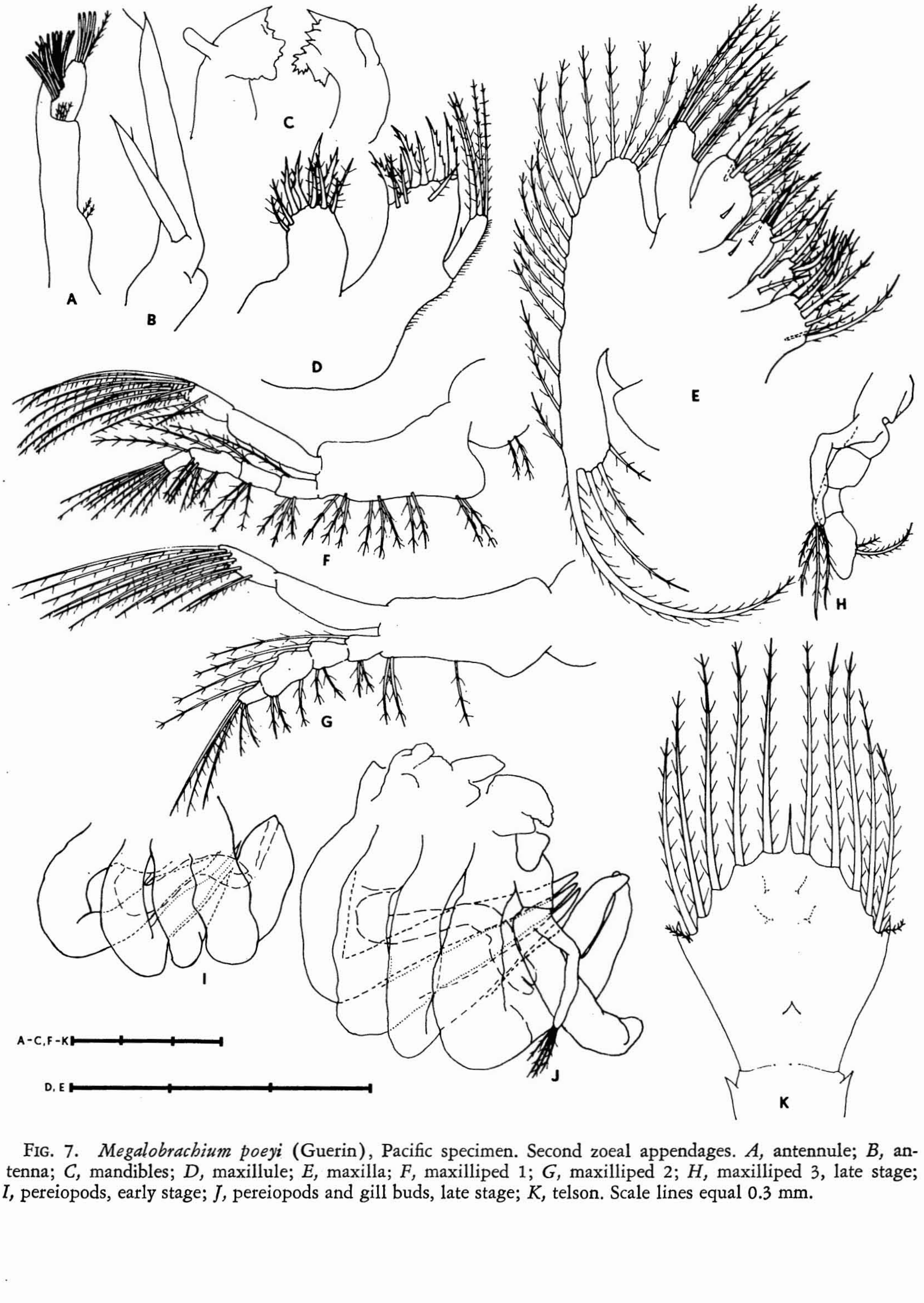

FIG. 7. *Megalobrachium poeyi* (Guerin), Pacific specimen. Second zoeal appendages. *A*, antennule; *B*, antenna; *C*, mandibles; *D*, maxillule; *E*, maxilla; *F*, maxilliped 1; *G*, maxilliped 2; *H*, maxilliped 3, late stage; *I*, pereiopods, early stage; *J*, pereiopods and gill buds, late stage; *K*, telson. Scale lines equal 0.3 mm.

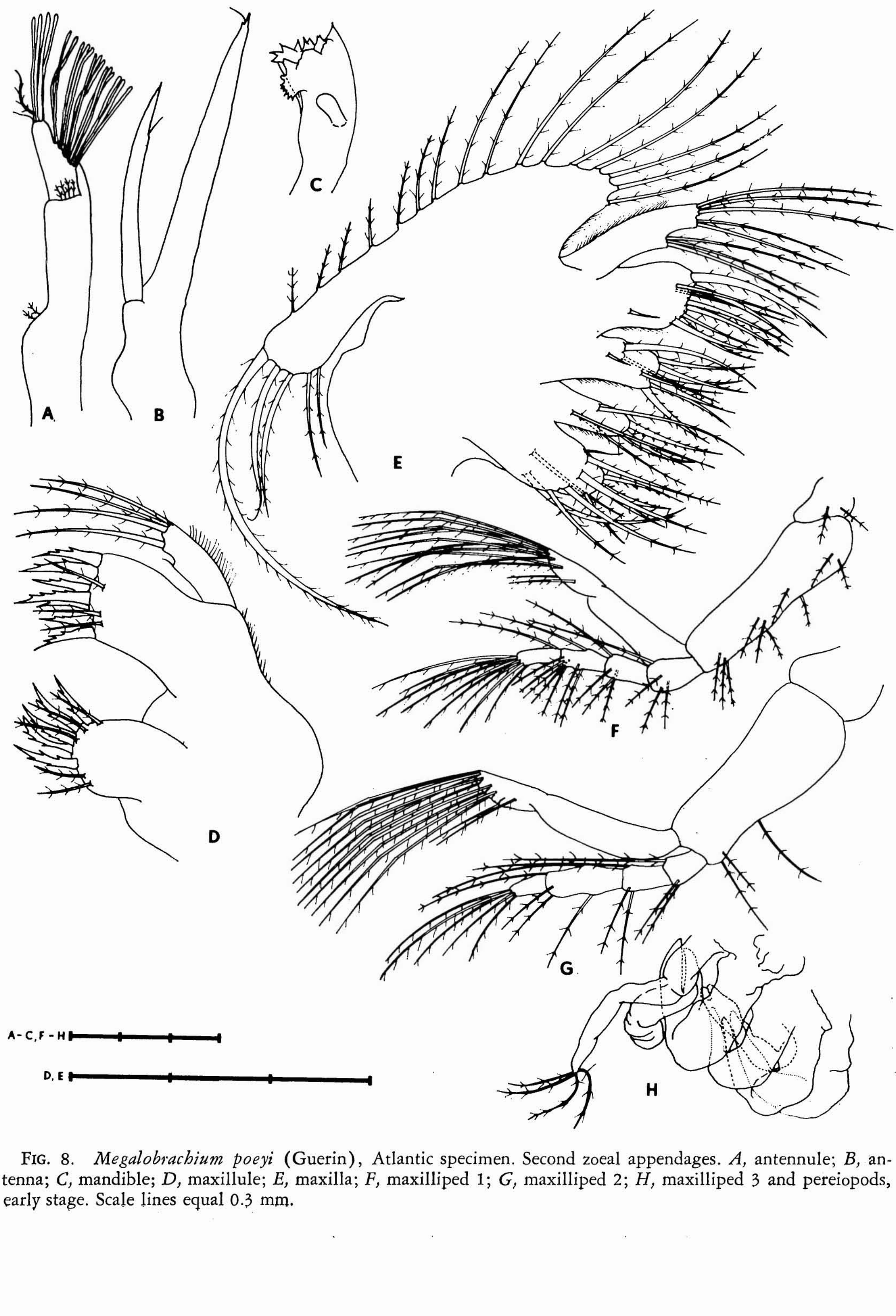

FIG. 8. *Megalobrachium poeyi* (Guerin), Atlantic specimen. Second zoeal appendages. *A,* antennule; *B,* antenna; *C,* mandible; *D,* maxillule; *E,* maxilla; *F,* maxilliped 1; *G,* maxilliped 2; *H,* maxilliped 3 and pereiopods, early stage. Scale lines equal 0.3 mm.

ventrally and serrations on plumose setae, remain as in stage I. [A: as above but larger].

COLOR: Chromatophores distributed and colored as in stage I. As noted for some other porcellanids (Gore, 1968, 1970) rostral spine becomes diffused with orange pigment when molt is imminent.

MEGALOPA

Carapace Length × Width

Carapace length × width is 1.1 × 1.2 mm [A: 1.3 × 1.4 mm].

Number of Specimens Examined

Ten [A: 10] specimens were examined.

CARAPACE (Figs. 3 and 4, *C, D*): Subovate, moderately inflated, minutely punctate and tuberculate, sparsely covered with short hairs dorsally and laterally which often trap detrital particles, making megalopa appear more hirsute than is actually the case. Frontal region prominent, not much deflexed, appearing transverse in dorsal view, extending beyond eyes; margin with usually 15 distinct curved hairs [A: 20–24 distinct spines plus more than 15 curved hairs] along anterior edges. Eyes disproportionately large; each eye with distinct cluster of granules on outer dorsal surface from which several thin hairs project (Fig. 3, *F*). A lateral ridge extends from epibranchial angle to posterior region, armed with several small widespread denticles on edge [A: denticles appear more prominent]. Outer orbital angle produced into small distinct tooth.

ANTENNULE (Figs. 9 and 10, *A*): Biramous; peduncle three-segmented, basal segment enlarged, rounded. Lower ramus with setae as shown (may vary slightly in both forms); three segmented. Upper ramus six-segmented; aesthetascs on segments two through five in the following sequence of rows and numbers: one row (5) [A: 6], two rows (3, 3 + 2 setae), two rows (3 + 1 seta, 2) [A: may be 3, 2 + 1 seta], one row (3). Other setae which may vary slightly in number as illustrated.

ANTENNA (Figs. 9 and 10, *B*): Peduncle three-segmented. Flagellum with two elongate, fused segments followed by 18–21 [A: 23 or 24] shorter segments bearing several short setae, including terminal segment with setae as shown.

MANDIBLES (Figs. 9 and 10, *C*): Now double-bladed scoops. Three-segmented palp, basal segment with two setae on distal edge, distal segment with about 11 [A: 14–15] short spines and setae as shown.

MAXILLULE (Figs. 9 and 10, *D*): Endopodite unsegmented, naked except for one subterminal seta shown. Coxal endite extended into rounded lobe, fringed with very fine hairs; 18–20 [A: ca. 25] processes as shown. Basal endite with 13 [A: up to 17] spines and 8–9 [A: ca. 10] setae as illustrated.

MAXILLA (Figs. 9 and 10, *E*): Endopodite incompletely two-segmented, with three setae as shown [A: may have one at base of endopod]. Coxal, basal lobes with major processes progressing toward endopodite as follows: 12 [A: 13] plus 14 [A: 16] encircling lobe; 5 spines, 8 setae [A: 6, 10]; 15 [A: 18]; 27–28 [A: ca. 30]; plus additional smaller setae as shown. Numbers in both forms occasionally vary by 1 or 2. Scaphognathite with 49–50 [A: 56–63] setae around edge, plus two small stubby setae on each side as shown.

MAXILLIPED 1 (Figs. 9 and 10, *F*): Setae as follows: exopodite, 2–3 stubby spines plus 5–6 setae terminally and laterally, very fragile; endopodite, 2 [A: 1 or 2]; protopodite, at least 40 [A: at least 50 or more]; all placed as shown.

MAXILLIPED 2 (Figs. 9 and 10, *G*): Exopodite two-segmented, with 11–13 [A: 14 or more] setae. Endopodite four-segmented, major setae progressing distally 7, 5, 13–16 [A: ca. 22], at least 16. Basipodite and coxopodite with 8 and 4 [A: 10, 3 or more] setae respectively. Other minor setae as shown.

MAXILLIPED 3 (Figs. 9 and 10, *H*): Coxal lobe with distal hook-shaped process, a distinct small spine and about 8 [A: 10] setae. Basal lobe with setae as shown. Processes on five-segmented endopodite as follows: ischium, about 18, plus one or rarely two small distinct

FIG. 9. *Megalobrachium poeyi* (Guerin), Pacific specimen. Megalopal sensory and feeding appendages. *A*, antennule; *B*, antenna; *C*, mandible; *D*, maxillule; *E*, maxilla; *F*, maxilliped 1; *G*, maxilliped 2; *H*, maxilliped 3. Not all setae completely illustrated. Scale lines equal 0.3 mm.

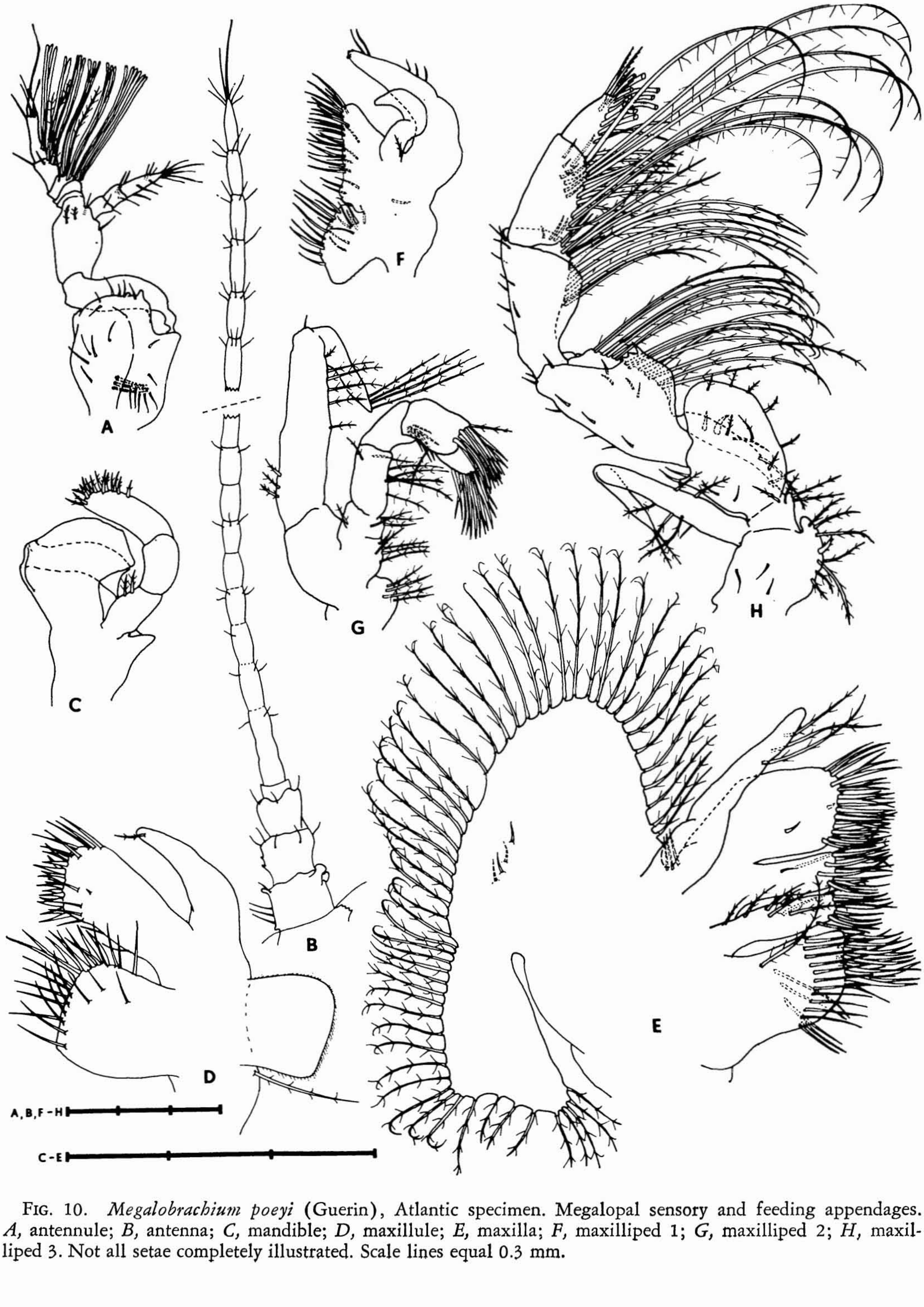

FIG. 10. *Megalobrachium poeyi* (Guerin), Atlantic specimen. Megalopal sensory and feeding appendages. *A,* antennule; *B,* antenna; *C,* mandible; *D,* maxillule; *E,* maxilla; *F,* maxilliped 1; *G,* maxilliped 2; *H,* maxilliped 3. Not all setae completely illustrated. Scale lines equal 0.3 mm.

spines; merus, about 13 large plus many small setae; carpus, 5–7 long spines, plus other setae as shown; propodus 7–9 stout spines, plus about 14 long setae; dactylus, 3 spines, plus 4 small, 8 long setae. Ischium, merus, carpus, with thin, platelike extensions; spines on ischium placed interior to plates. Exopodite with setae as shown. In the Atlantic form the processes in the above sequence are: 16, plus 2 small spines; 13–14 large setae; 9–11 long spines, 13 long setae; 10 stout spines, 16 long setae; 5 spines, 9–10 long setae. Outer carpal plates produced into 1–3 blunt teeth; these teeth less developed or lacking in Pacific form. Exopodite as illustrated.

PEREIOPODS (Figs. 3 and 4, *C* and *E;* 11, *C* and *D*): Chelipeds large, flattened, nearly equal, covered with setae. Carpus of cheliped with distinct spines on anterior edge, blunt curved teeth on posterior edge, as shown. Outer edge of hand and finger distinctly dentate. All spines and teeth more pronounced in the Atlantic form. Walking legs as illustrated; merus, carpus and propodus with one to three very small blunt teeth dorsally, propodus with pair of movable spines at distal edge. In Atlantic megalopae the dorsal and ventral edges of walking legs 3–1 armed with 3–10 or more small, but distinct teeth or spines, as illustrated. Dactylus in both forms with three accessory

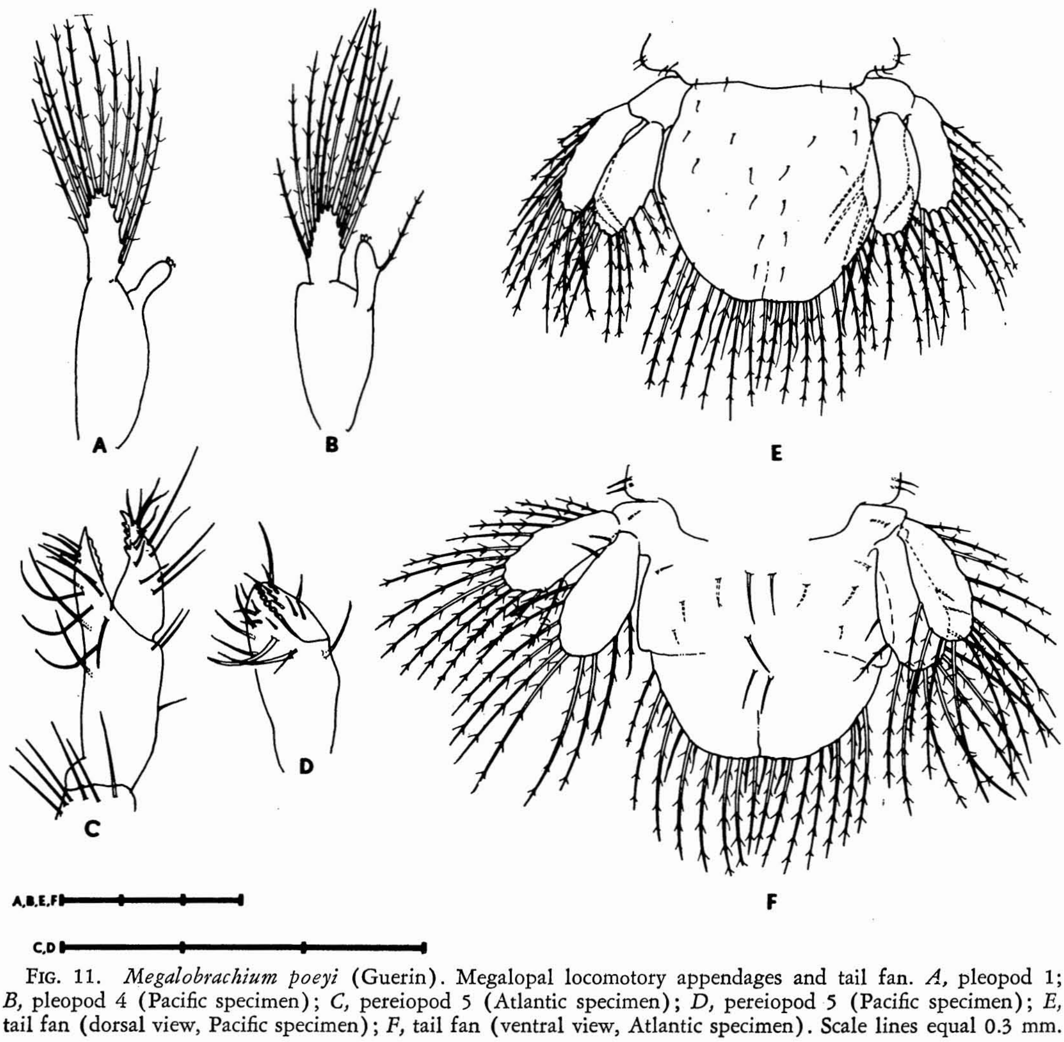

FIG. 11. *Megalobrachium poeyi* (Guerin). Megalopal locomotory appendages and tail fan. *A,* pleopod 1; *B,* pleopod 4 (Pacific specimen); *C,* pereiopod 5 (Atlantic specimen); *D,* pereiopod 5 (Pacific specimen); *E,* tail fan (dorsal view, Pacific specimen); *F,* tail fan (ventral view, Atlantic specimen). Scale lines equal 0.3 mm.

spinules. Pereiopod 5 chelate, gape dentate; many short spines and several long setae as shown.

PLEOPODS (Fig. 11 *A, B*): As illustrated, biramous, decreasing in size toward telson. Exopodal setae inconsistent; from 10–13 setae and variable on each side. Endopodite nearest telson with one seta, others usually naked [A: endopodite setae progressing toward telson vary from 0, 0, 0, 1 to 0, 1, 1, 2]; all have small hooks as appendix interna.

ABDOMEN (Figs. 3 and 4, *C*): Abdominal pleura with setae as shown, numbers inconsistent.

TELSON (Fig. 11 *E, F*): Usually 8 + 8 long plumose setae plus additional shorter processes as shown. Numbers inconsistent. Uropods biramous, exopodites with about 13 setae, endopodites with 8–10 setae, around distal edges. Atlantic megalopae have consistently 2–4 more setae in each case.

COLOR: Eyes iridescent green. Body transparent at this stage but setae collect detrital particles imparting white to tan color. Red chromatophores placed as follows: dorsally on cheliped and walking legs, at junction of carpus and propodus; ventrally on coxae of pereiopods and maxilliped 3. Orange chromatophores internally on mouthparts, especially maxillule, maxilla and maxillipeds 1–3.

DISCUSSION

Consideration of the Larvae

It is apparent from the description and illustrations just provided that the zoeae and megalopae of the amphi-Panamanian forms of *Megalobrachium poeyi* are similar in many respects. The Atlantic and Pacific larvae agree well in features such as coloration, duration of larval development (see Table 1) and larval survival. The zoeal appendages of both forms are similar in form and setation. Nevertheless, sufficient morphological differences exist, chiefly in the carapace spines and number of setae on some mouthparts in the zoeal stages and in the carapace, chelipeds, and pereiopods of the megalopal stage, to warrant discussion. A summary of these variations is presented in Tables 2 and 3.

The differences in carapace and appendage armature in the zoeal stages of the two geographical forms allow the larvae to be easily distinguished from each other. For example, the elongate rostral spine of the zoeae from the Pacific adult had fewer (4–7) ventral spinules than the zoeae from the Atlantic adult (12–18). The zoeal mouthparts of the latter appear to have longer and better developed processes than those from the Pacific crab. Setal counts were also generally higher on appendages of zoeae from the Atlantic crab.

The number and position of most appendage processes of individual zoeae in each stage were usually consistent, although variation by one or two setae rarely occurred. This variation has been noted in the preceding description. The differences in the appendages of zoeae from each region, however, were also notably constant (see Table 2). Such variations may prove taxonomically significant when used in conjunction with differences in carapace spination, since the zoeal stages of Atlantic and Pacific crabs may then be distinguished.

The megalopae of the two forms have more pronounced differences than the zoeal stages and are also easily separated (see Table 3). Megalopae from Atlantic crabs are larger and have, among other features, increased spination on the carapace frontal region, more prominent spines on the chelipeds and walking legs, more antennal segments, and greater numbers of long plumose setae on the maxillipeds. These features appeared to be consistent in the specimens examined.

Several features present in the megalopae of both forms are not found in the adults. In the megalopae of both forms the frontal region is straight, not deflexed or trilobate as in the adult. The large distinct spines present on the carpus and hand of the chelipeds in the megolapae are lacking in the adults. The dorsal surface of the walking legs, armed with many distinct spinules in the Atlantic form or with few or none in the Pacific specimens, is unarmed in adults from either geographical region. The legs of the adults are, instead, heavily covered with hairs which trap detrital particles. The megalopal carapace is lightly punctate and covered sparsely with nonplumose hairs, whereas in the adults it is roughly granular and

TABLE 2

COMPARISON OF ZOEAL FEATURES IN ATLANTIC AND PACIFIC SPECIMENS OF *Megalobrachium poeyi*

	PACIFIC FORM	ATLANTIC FORM
ZOEA I		
Carapace		
Length	1.01 mm	1.41 mm
Rostral Spine	2.5 × carapace length 5–7 ventral spinules	2.9 × carapace length 12–14 ventral spinules
Posterior Spine	1.5 × carapace length 4–6 ventral spinules	2.0 × carapace length 12–14 ventral spinules
Antenna		
Exopodite	slightly longer than endopodite	1/4 × longer than endopodite
Maxilla		
Basal Endite	7–8, 7 processes	7–8, 8–7 processes
Coxal Endite	7, 4–5 processes	7–8, 4–5 processes
Scaphognathite	6 + 1 apical setae	6–7 + 1 apical setae
ZOEA II		
Carapace		
Length	1.2 mm	1.6 mm
Rostral Spine	1.7 × carapace length 4–7 ventral spinules	3.5 × carapace length 18 ventral spinules
Posterior Spine	1.6 × carapace length 3–4 ventral spinules	2.0 × carapace length 8–10 ventral spinules
Antenna		
Exopodite	1/2 length of endopodite	ca. 3/5 length of endopodite
Maxilla		
Basal Endite	8, 10 processes	10, 10 processes
Coxal Endite	10, 6 processes	10–11, 6 processes
Scaphognathite	19 + apical setae	20 + apical setae

covered with plumose and nonplumose hairs. Thus, while the known megalopal stage of most porcellanids so far investigated approximates the adult form, such is not completely the case with *M. poeyi.* And, although features just mentioned were present as late as crab stage 3 (the latest stage attained in rearing), it was impossible to determine at which stage they began to be lost. One Pacific crab 3 did not have the prominent spines on the carpus of the chelipeds though they were present in its crab 2 exuvia.

Laboratory-cultured larvae from the Atlantic crab were longer than those obtained from the Pacific specimen. Although size differences permit separation of cultured Atlantic and Pacific larvae they may prove less reliable when compared with specimens collected from nature, because the identical stage of the plankton counterpart may be somewhat larger (see Leroux, 1966). Consequently, the size of cultured larvae may not reflect the "true" size of zoeae and megalopae in the plankton from either region.

Previously laboratory-cultured porcellanid larvae are, as far as is known, identical with larvae of the same species collected from the plankton, except for size. There is no reason to assume otherwise for the cultured larvae of *M. poeyi.* Unfortunately, only a single hatching was obtained for each geographical form and no specimens are available from the plankton. Without such specimens, or larvae from another hatching, and a longer series of early crab stages, no firm conclusions regarding the observed morphological variations in zoeae and megalopae can be drawn (see below).

Considerations of the Adults

The adults of *M. poeyi* are morphologically indistinguishable and are presently considered to be conspecific, though their larvae may easily be separated. It appears unlikely that the adults are either separate or analogous species because there does not seem to be any salient morphological feature by which the two forms may be separated. An earlier description (Haig, 1960, p. 214) of the Pacific species fits the Atlantic specimens equally well. Moreover, the adult crabs noted herein were sent to Miss Janet Haig of the Allan Hancock Foundation and she confirmed the species identification. She stated (personal communication) that, on the basis of adults, the two populations should be considered conspecific though larval differences were "remarkable."

It is possible that the two forms may be subspecies. The criteria for such requires that a distinct geographical area be occupied and the population have distinctive features which differ taxonomically from other populations. In this case, although the two adult forms presumably are geographically separated on either side of Panama, they remain morphologically indis-

TABLE 3

COMPARISON OF MEGALOPAL FEATURES IN ATLANTIC AND PACIFIC SPECIMENS OF *Megalobrachium poeyi*

	PACIFIC	ATLANTIC
Carapace		
Length × width	1.1 × 1.2 mm	1.3 × 1.4 mm
Frontal Region	15 curved hairs	24 distinct spines + hairs
Antennule		
Aesthetascs	5, 3, 3 + 2 Setae, 2 + 1 Setae, 3	6, 3, 3 + 2 Setae, 2 + 1 Seta, 3
Antenna		
Segments	18–21	23 or more
Mandibles		
Palp Segment 3	11 spines and setae	14–15 spines and setae
Maxillule		
Endopodite	1 subterminal seta	1 subterminal seta
Coxal Endite	18–20 processes	ca. 25 processes
Basal Endite	ca. 13 spines, 8 setae	ca. 17 spines, 10 setae
Maxilla		
Endopodite	3 staggered setae	3 staggered setae
Coxal Endite		
Proximal Lobe	12, + 14 encircled setae	13, + 16 encircled setae
Distal Lobe	5 + 8 processes	6 + 10 processes
Basal Endite		
Proximal Lobe	15 processes	18 processes
Distal Lobe	27–28 processes	30 or more processes
Scaphognathite	47–50 processes	56–60 processes
Maxilliped 1		
Exopodite	5–6 terminally	5 laterally and terminally
Endopodite	2 setae	1–2 setae
Protopodite	at least 40 setae	at least 50 setae
Maxilliped 2		
Exopodite	1 + 5 lateral setae	3 + 6 lateral setae
Endopodite		
Propodus	at least 13 processes	ca. 22 processes
Dactyl	at least 10 processes	15 or more processes
Maxilliped 3		
Endopodite		
Ischium	usually 1 small spine	2 small spines
Merus	13 long setae	13–14 long setae
Carpus	5–7 long spines	9–11 long spines
Propodus	14 long setae	16 long setae
Dactylus	3 spines, 8 long setae	5 spines, 9–10 long setae

tinguishable. It is presently impossible to determine whether they may be distinguished taxonomically solely by their respective larvae. A major difficulty arises in attempting to identify the adults to a correct subspecies if no larvae are available. In such a case, geographical separation, admittedly a tenuous criterion in this instance, would be the only means of identification, and locality data would be essential.

Because of the several problems inherent with the adults, as well as the limited larval and juvenile series available, there is insufficient evidence to establish any subspecies at this time. To do so would require examination of all adult specimens plus that of a long series of megalopae and juvenile crabs. The former is time-consuming and the latter, at present, impossible. It would seem, however, that the apparent geographical isolation of the adults on either side of the Panamanian isthmus, plus the differences exhibited in the zoeal and megalopal stages of the two forms, is sufficient ground to question the present conspecific status of the adults.

Comparison of M. poeyi *Larvae with Larvae of Other Species*

The zoeal stages of the Porcellanidae, whether cultured or collected from the plankton, have usually been separated into two major categories as originally derived by Lebour (1943, 1950). The categories rely chiefly on the position of the processes on the telson in both zoeal stages. In the one group (*Porcellana, Pisidia, Polyonyx, Euceramus*) the fifth pair of plumose setae are not located on the central prominence of the telson in the first stage; whereas, in the second stage, a sixth pair of setae are added in this position. In the second group (*Petrolisthes, Pachycheles*) the fifth pair of plumose setae are situated on the central prominence in the first zoea, and a single median spine appears here in the second zoea. *Megalobrachium poeyi* exhibits telson features which place it in the second grouping. I am disregarding at present some western Pacific *Petrolisthes* species that exhibit features which would place them in the *Porcellana* et al., section. These species possess somewhat anomalous features as adults with respect to the genus *Petrolisthes* and their larvae will probably have to be placed in a third grouping.

The distinctions between the known zoeae of the genera mentioned above (excluding *Megalobrachium*) have been dealt with at length elsewhere and will not be discussed further here (see Wear, 1964*a, b;* Greenwood, 1965; Knight, 1966; Boschi, Scelzo, and Goldstein, 1967; Gore, 1968, 1970; Roberts, 1968).

Megalobrachium poeyi zoeae can be presently recognized by the following characteristics: the limited number of ventral spinules on the rostral and posterior carapace spines, antennal exopodite 1/4 times longer to 1/2 times less the length of the endopodite, by the high total number of setae (2 + 5 or 6) present on the interior border of the third segment of the first maxillipeds, and by the telson features mentioned above. The distinct curvature of the rostral spine is tentatively included here, to be used in conjunction with the other features, pending further investigation.

The zoeae of the genus *Megalobrachium,* if typified by *M. poeyi* zoeae, may be distinguished by the rostral spine and perhaps by the previously mentioned number of setae on the first maxillipeds. Both features are easily noticed on *M. poeyi* larvae. In the Atlantic, *Petrolisthes armatus* and *Pachycheles haigae,* the only two members of the *Petrolisthes* group for which larvae are presently known, have a total of six or seven setae (2 + 4 and 3 + 4, respectively) on the first maxilliped position. However, the larvae of these species both have relatively straight rostral spines, heavily armed overall with many spinules, plus more and/or larger spinules on the posterior carapace spines. The antennal exopodite of *Petrolisthes armatus* has two setae subterminally in both zoeal stages whereas that of *Pachycheles haigae* has three heavy spinelike processes in the first stage and is naked in the second stage (see Gore, 1970; Boschi, Scelzo, and Goldstein, 1967). The antennal exopodite of *M. poeyi* has one subterminal seta.

Zoeae of *Pachycheles rudis,* the only species of the *Petrolisthes* group in the eastern Pacific from which larvae have been cultured, have only five setae (2 + 3) ventrally on the third segment of maxilliped 1, heavily armed rostral and posterior carapace spines, three curved hooks on the antennal exopodite (first zoea); the exopodite is naked in the second zoea (Knight, 1966). These features make *P. rudis* larvae easily distinguishable from *M. poeyi* zoeae.

In an earlier paper (Gore, 1968) I suggested that the dorsal setae on the carapace might aid in identification of zoeae, but study on zoeae of other genera suggests that this feature is unreliable (Gore, unpublished data).

The megalopae of *M. poeyi* may be recognized by the spines on the anterior edge of the carpus of the chelipeds, by the distinct curved hairs (or hairs plus spines) on the frontal region, by the cluster of tubercles on the eyes and, in the Atlantic form at least, by the many spinules on the dorsal and ventral surfaces of the pereiopods. The two geographical forms may be further separated by features discussed earlier. Because the megalopa of *M. poeyi* does not resemble the adult in many features, it does not seem feasible at present to suggest characters which might enable megalopae of other species of the genus to be recognized in the plankton.

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